type of animal life the *absence* of which was characteristic of a particular district or region. This term he proposed should be "Lipotype"[1].

Thus the order Insectivora and the families Bovidæ and Viverridæ were "lipotypes" of the Neotropical Region; the Bears (Ursidæ) and the Deer (Cervidæ) of the Æthiopian Region; and the Woodpeckers (Picidæ) and Vultures (Vulturidæ) of the Australian Region.

The term was of course more specially required and more appropriate in cases where the "lipotype" was a form that might *primâ facie* have been expected to occur in the Region or district in question but was remarkable by its absence.

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Dr. Günther, F.R.S., exhibited a flat skin of a very remarkable pale sandy-coloured variety of the Leopard (*Felis pardus*), from the Matabele district, South Africa, and pointed out its superficial resemblance in colour to the Woolly Cheetah (*Felis lanea*, Sclater).

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Dr. Günther also exhibited and made remarks upon the shell of a new Tortoise of the genus *Geoemyda* from Siam, which he proposed to describe as new at a subsequent meeting.

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Mr. R. Bowdler Sharpe exhibited a specimen of a Goldfinch from Hungary, which had been sent to him by Dr. J. von Madarasz of the Museum of Buda-Pest, and which had been described by that gentleman as *Carduelis elegans albigularis*. Mr. Sharpe pointed out that a variety of the Goldfinch with a white throat was by no means unplentiful in England, and that a figure agreeing with the specimen now exhibited would be found in the late Mr. Dawson Rowley's 'Ornithological Miscellany' (vol. i. p. 91, fig. 3 in the plate).

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The following papers were read:—

1. On some Points in the Anatomy of *Pterocles*, with Remarks on its Systematic Position. By Hans Gadow, Ph.D., C.M.Z.S.

[Received February 18, 1882.]

Amongst the unfinished manuscripts of the late Prof. A. Brandt, in St. Petersburg, there were some notes by him preparatory to a discussion on the anatomical characters of the *Pterocletes*. His son, now Professor in Charkow, was good enough to put these notes into my hands, while others were distributed amongst those naturalists who specially interested themselves in the other different groups to which that distinguished naturalist had devoted some of his attention. The Society will see, therefore, that it was with peculiar

[1] λείπω, *deficio*, et τύπος, *forma*.

pleasure that a specimen of *Pterocles arenarius* in the flesh was received by me during the short time that I was intrusted with the duties of its prosector during his absence from England[1].

## Integument.

The arrangement and form of the feather-tracts in *Pterocles* and *Syrrhaptes* is almost the same as that in the Pigeons; but too much weight has been laid upon the peculiar bifurcated shape of the shoulder part of the spinal tract. Nitzsch himself, in his description of the Gallinacei, mentions that a very similar arrangement of the shoulder-tract we meet with in *Numida* and *Penelope* and partly in *Tetrao* and *Crypturus*. He points out that in this respect *Numida* in particular approaches the Columbine type.

Again, the Charadriidæ and many Laridæ present nearly the same type of feather-tracts, although they differ in the lower and ventral part of the spinal tract.

The contour-feathers of *Pterocles* possess a very small after-shaft, whilst this organ, although likewise small, is present in the Limicolæ and Gallinacei, but altogether absent in the Pigeons.

The number of the rectrices and of the primaries is of no systematic importance in these birds, as will be seen from the following table:—

| | Total number of quills. | Primaries. | Which of the primaries the longest. | Number of rectrices. |
|---|---|---|---|---|
| Pterocles ..... | 27–28 | 10 | first | 16 |
| Pigeons ..... | up to 25 | 10 | second | 12, 14, 16 |
| Plovers ..... | 24–26 | 10 | first | 12 |
| Fowls ..... | 22–29 | 10, 11 | 4th, 5th, 6th | 10–20 |

[1] Principal books and essays referred to in the text:—

W. K. Parker. "On the Osteology of Gallinaceous birds and Tinamous," Trans. Zool. Soc. v. pp. 149–241.

A. H. Garrod. "On certain Muscles of the Thigh of Birds &c.", P. Z. S. 1873, pp. 626–677, and 1874, pp. 111–123.

——. "On the Disposition of the deep Plantar Tendons in different Birds," P. Z. S. 1875, pp. 339–348.

——. "On the Carotid Arteries of Birds," P. Z. S. 1873, pp. 457–472 (for *Pterocles* see p. 468).

——. "Nasal Bones of Birds," P. Z. S. 1873, pp. 33–38 (*Pterocles*, see pp. 36, 37).

Nitzsch. 'System der Pterylographie,' 1840.

E. Blanchard. "Caractères ostéologiques des Gallinacés ou Gallides," in Ann. Sciences Natur. sér. 4, tome vii. (1857), pp. 91–106, plates 10–12.

M. Oustalet. "Monographie des Oiseaux de la famille des Megapodiides," *Op. cit.* sér. 4, tome x & xi. (1881).

H. Gadow. "Beiträge zur vergleich. Anat., Verdauungssystem d. Vögel," Jenaische Zeitschrift, 1879.

Bogdanow. In 'Mélanges biologiques,' 1880, pp. 49–55.

D. G. Elliot. "A Study of the Pteroclidæ or Family of the Sandgrouse," P. Z. S. 1878, p. 233–264.

The *general coloration* of the Sand-Grouse is thoroughly protective, and is very distinctly marked throughout the genus by the dark crescent on the breast and the dark colour of the under surface of the wings. Though pronounced and apparently peculiar to the Sand-Grouse, a similar pattern is found in some of the Pigeons, as well as in the Plovers and in Grouse.

The *nestling plumage* of the Sand-Grouse consists of a thick downy cover with fine terminal hairs to each down-feather, much like that of the Plovers and Fowls, whilst the Pigeons, when hatched, are almost nude and are entirely devoid of downy feathers.

The *oil-gland* is present and quite naked in Sand-Grouse and Pigeons (in some Pigeons wanting), whilst in the Gallinacei and Limicolæ this organ is tufted.

In both form and structure the "tarsus" and the claws of the Sand-Grouse closely resemble those of the Gallinacei, but are remarkable for the tendency to suppression of the first or hind toe, which in *Syrrhaptes* is entirely aborted. This never occurs amongst the Pigeons and Fowls, but is a common feature in the Pluvialine tribe.

The *bill* and the *nostrils* of *Pterocles* are like the same parts in the Turnicidæ, which, like *Pterocles* and the Columbæ, are schizorhinal, whilst the Rasores proper are what Garrod termed holorhinal.

## Osteology.

As the osteology of *Pterocles* and *Syrrhaptes* has been fully described by Professors Parker and Garrod, it will be superfluous for me to do more than indicate some of the salient points. Prof. Parker says:—"There is no vomer in the *Syrrhaptes* to tie the two palatines together; and this is a sudden assumption of a columbaceous character." However, this is not of great importance, because most of the Tetraonidæ have also no vomer, or at least this bone is very much suppressed.

The skull certainly bears many striking affinities to the Columbæ. The *Syrrhaptes* keeps close to the Fowls in respect of its vertebral characters.

| | Number of cervical vertebræ. | Dorsal. | Sacral. | Caudal. |
|---|---|---|---|---|
| *Syrrhaptes* | 16 | 4 | 15 | 6 |
| *Pterocles arenarius* | 15 | 5 | 15 | 7 |
| *Columba livia* | 14 | 4 | 14 | 7 |
| *Gallus** | 16 | 4 | 15 | 6 |

"There is much that is Pigeon-like in the pelvis of the Grouse and the *Syrrhaptes*."

All the wing-bones, and in particular the humerus, strikingly resemble those of the Pigeons (see Garrod, P. Z. S. 1874, p. 255, fig. 1).

## Muscular System.

I myself have examined specially only the muscles of the pelvic region and those of the hinder extremity. As regards the

* Parker, *l. c.*

muscles of the shoulder-girdle I am indebted to Prof. Fuerbringer for the information that *Pterocles* approaches nearer to the Pigeons than to the Fowls.

*Mm. iliaci externi* (*mm. glutei*).—This group in *Pterocles* consists of only two muscles, an anterior and a posterior. Of these the latter is the larger; it arises from the broad latero-dorsal plane of the præacetabular part of the ilium, and is inserted close to the external trochanter of the femur. The iliac muscles have their nerve-supply from the crural plexus.

*M. iliacus internus.*—This small muscle is comparatively long, as it arises from nearly the middle of the ventral aspect of the præacetabular ilium. It is inserted as usual, between the internal trochanter and the neck of the femur.

*M. sartorius.*—Flat and very broad, from the greater part of the lateral and dorsal margin of the præacetabular ilium. The muscle is partly blended with the *m. ilio-tibialis* at the distal third of the thigh; the rest passes over the patella as a flat but nevertheless rather fleshy strip, and then extends into part of the head of the m. extensor digitorum communis. The muscle is supplied by nerves from one of the first branches of the crural plexus.

*M. ilio-tibialis* (m. quadratus femoris).—This muscle is rather feebly developed; it arises with an aponeurotic sheet, which superficially covers the mm. iliaci externi, and which also takes origin from the regio posttrochanterica of the ilium. The muscle is completely blended with the m. femoro-tibialis, with the m. gluteus posterior, and with the m. sartorius. It is inserted together with the tendon of the mesial and external part of the m. femoro-tibialis into the head and rest of the tibia. Nerve-supply from the crural plexus.

The *m. gluteus posterior* + *m. tensor fasciæ latæ* (m. tensor fasciæ latæ) arises rather fleshy from the lateral plane of the postacetabular part of the ilium, and is inserted indirectly into the head of the tibia by being attached to the distal part of the m. ilio-tibialis. Nerve from the ischiadic plexus.

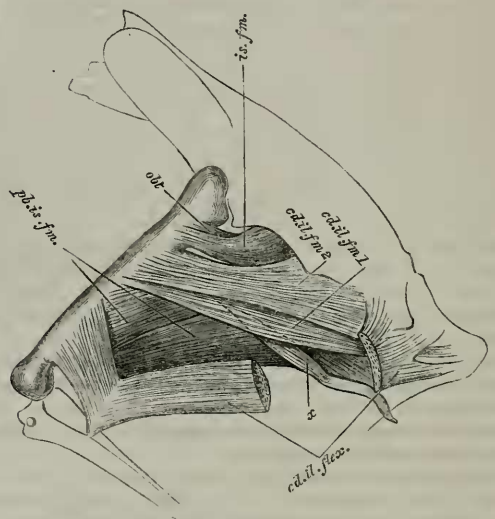
The *m. gluteus anterior* (m. gluteus quartus) is very small; its muscular part consists of only a few fibres. Its aponeurosis arises from the space left between the origin of the m. iliac. ext. post. and the antitrochanter. Its short but broad and flat tendon runs over the external trochanter, passes the tendons of the external iliac muscles, and is inserted just distad from their insertion into the outer aspect of the femur. The nerve to this muscle is given off from the pl. ischiadicus; it passes round behind the antitrochanter out of the ischiadic foramen.

The *m. ambiens* arises with a short and distinct tendon from the pubic spine; its roundish and somewhat ribbon-shaped belly tapers out into a long slender tendon, which, after partly piercing that of the m. femoro-tibialis, passes over the knee into its outer side and then supports one of the heads of the m. flexor perforatus digiti III. Between the proximal part of the ambiens muscle and the inner trochanter of the femur, that long nervous branch which is sent off

from the posterior part of the crural plexus passes out, and then runs along the inner side of the thigh, superficially to the inner side of the proximal end of the leg (Ruge's branch, as termed by me in my paper on the Ratitæ). The ambiens muscle, on account of its nervous supply, belongs to the crural plexus, as the nerve of this muscle is one branch of the large nervous stem which passes laterally from the m. ambiens into the inner head of the m. femoro-tibialis (m. rectus internus femoris).

The *m. femoro-tibialis* (mm. vasti or m. cruræus) consists of three heads. The inner one (m. rectus internus femoris) is the biggest and most distinct; it arises from the whole inner and hinder aspect

Fig. 1.




Deeper adductor muscles of the right thigh of *Pterocles arenarius*

of the femur, and is inserted, independently of the others, into the anterior crest of the tibia. The middle head is also very fleshy, arises from nearly the whole of the anterior aspect of the femur, takes up the distal part of the m. ilio-tibialis, and is inserted into the patella and into the head of the tibia. The third or outer head is quite separate from the others, and is inserted into the outer edge of the caput tibiæ by the help of the ligamentum tibio-patellare. All these three heads are supplied by nerves from the crural plexus.

The *m. ilio-fibularis* (m. biceps) takes its origin from the lateral

margin of the postacetabular ilium and from the lateral plane of the distal half of this bone. Its tendon passes through the tendinous loop near the poplitea, and is inserted into the neck of the fibula. Its nerves come from the ischiadic plexus.

*M. caudæ ilio-flexorius* (m. semitendinosus). See fig. 1. This ribbon-shaped muscle arises from the lateral processes of some of the first caudal vertebræ and from the outer plane of the spina ilio-caudalis. The so-called accessory part of this muscle is well developed; it descends from the outer and lower surface of about the distal third of the femur; and its fibres join those of the long or main part nearly at right angles. The line of junction is indicated by an oblique tendinous raphe. The two combined parts are inserted, first into the neck of the tibia by a strong tendon; secondly, a small tendon, looking like the continuation of the raphe, descends superficially to the back of the leg and joins the caput femorale internum m. gastrocnemii. Nerve-supply, together with the next muscle, from the ischiadic plexus.

The *m. ischio-flexorius* (m. semimembranosus) is feebly developed, and loses its independence by becoming blended with the m. caudæ ilio-flexorius, which completely covers it externally. It arises from a small part of the middle line of the lateral margin of the ischium.

The *m. caudæ ilio-femoralis* consists of two chief parts. The most lateral one, or long head (long head of femoro-caudalis), is a very narrow, slender, muscular ribbon, which arises from the proc. lat. of the last caudal vertebræ, and is inserted by a narrow thin tendon into the latero-posterior plane of the end of the proximal third of the femur. Towards its insertion the fleshy part of this long head is to a great extent blended with the more proximal or greater part: the latter (accessory femoro-caudal) arises from part of the membrane of the foramen oblongum, and from the outer plane of the hindmost or distal part of the ischium, whilst only a few fibres arise from the adjacent part of the ilium. The nerve which supplies these two muscles comes from the ischiadic plexus, and passes externally over the m. ischio-femoralis. I must mention here a peculiar little muscular slip which I have not often observed in birds. It arises (see fig. 1) as a small fleshy flat slip from the outer aspect of that region where the pubis and ischium approach each other; it is then partly covered by the long head; its thin tendon unites with that of the long head. It was present also on the other side, and was supplied by the same nerve-branch together with the two large heads. The presence of this little muscular slip is an instance of the great variation to which this group of the m. caudæ ilio-femoralis is subject.

The *m. ischio-femoralis* (m. obturator externus) arises with fleshy fibres from the dorsal, distal, and ventral margins of the foramen oblongum; its strong tendon is inserted into the outer plane of the femur, just distad from the insertion of the m. obturator. It receives its nerve from the ischadic plexus.

The *m. obturator* arises from that part of the inner plane of the ischium which bounds the foramen obturatum and also from the

adjoining part of the pubis. It is inserted by means of a very strong tendon into the externo-posterior plane of the outer trochanter.

Another muscle, which we may call an accessory muscle to the m. obturator, is very small, and arises from the most proximal and lateral part of the ossa pubis et ischii near the acetabulum; its fleshy but short belly is separated from that of the m. ischio-femoralis by the tendon of the main obturator muscle. It is inserted just between the tendons of these two muscles. As this small muscle is not supplied by the pl. ischiadicus, but together with the m. obturator, we cannot consider it to be a representative of the gemelli muscles, nor of part of the m. obturator internus of mammals. But the m. obturator of birds, together with its accessory muscles, might correspond to the m. obturator externus of Mammalian anatomy.

The *m. pubi-ischio-femoralis* (m. adductor) consists of two layers, a lateral and more proximal and a median or distal one. The lateral part is ribbon-shaped, and arises from the latero-ventral margin of the middle third of the spines, opposite the pubis. It is covered laterally by the m. caud. ilio-femoralis, and is inserted into the hinder aspect of the distal half of the femur, lying mesiad from the femoral portion of the m. caudæ ilio-flexorius (femoral portion="accessory part"). The inner layer arises from the lateral margin of the distal two thirds of the ischium, but not from the os pubis or the ischio-pubic membrane. This flat muscle forms scarcely any tendon, and is inserted as a broad, but flat and vertical sheet into the distal half of the femur, including the internal condyle, and into the hinder surface of the head of the tibia.

The *m. popliteus* is developed as usual.

The *m. tibialis anticus* consists of two heads. The external or femoral is represented simply by a long tendon arising from the anterior inner margin of the internal condyle; its short belly soon fuses completely with the tibial or chief head, which latter takes its fleshy origin from the crest and head of the tibia. The strong tendon of this muscle passes under the transverse ligament of the leg, and is inserted into the anterior or dorsal sulcus of the tarso-metatarsal bone, not far from the joint. The whole muscle is covered superficially by the m. gastrocnemius (inner head) and by the m. peroneus superficialis. Nerve-supply, as in all the following muscles, from the ischiadic nerve.

*M. peroneus superficialis.*—The most superficial muscle on the anterior and outer side of the leg. It arises from the crest of the head and from the anterior plane of the neck of the tibia, and sometimes from the head of the fibula. Its broad tendon passes round the outer side of the leg to the hinder aspect of the intertarsal joint, and then divides into two tendons: one is very broad, and forms the deep sheet of the susceptaculum; the other one is much narrower, passes laterally over the external malleolus of the tibia, and then joins the tendon of the m. flexor perforatus dig. III.

A *m. peroneus profundus* was not present in my specimen of *Pterocles*. However, this muscle is subject to much variation. I found it well developed in *Euplocamus prælata*, but wanting in *Gallus*

*bankiva* and in *Penelope superciliosa*, whilst in our common Domestic Fowl it is generally present. In the Pigeons it is often absent. If present, this muscle arises with a long but narrow and fleshy belly from the anterior plane of the angle between the lower end of the fibula and the middle third of the tibia; its strong tendon then passes laterally over the joint and is inserted into the proximal margin of the plantar tarso-metatarsal bone, near the external malleolus. When contracted, the muscle bends the tarso-metatarsus slightly dorsad and inwards.

*M. gastrocnemius.*—This large muscle consists in *Pterocles* of two parts, each of which arises with two distinct heads (fig. 2):—

Fig. 2.

Lateral posterior view of the gastrocnemius muscle of right side of *Pterocles arenarius*.

I. Median part.
   *a. Cap. tibiale*: from inner and anterior aspect of the head and neck of the tibia, blending with the tendons of the m. femoro-tibialis.
   *b. Cap. femorale*: from hinder aspect of the intercondyloid region, and at the same time from the ligam. femoro-tibiale internum.

II. Lateral part.
   *a*. With a slender but distinct tendon from the intercondyloid region and from the outer margin of the femur; its belly

passes between the two principal branches of the ischiadic nerve, and is supported by the descending tendon of the m. semitendinosus = m. caudæ ilio-flexorius.

β. This head is the larger of the two, and is the most superficial one at the hinder and external aspect of the leg, as it arises from the external condyle of the femur. The "tendo communis" of these four heads is inserted into the hinder margin of the tarso-metatarsal bone, but principally into the tibial and median margin.

The *m. extensor digitorum communis* appears after the removal of the superficial peroneal and of the tibialis muscle, being completely covered by the latter. It arises from the anterior plane of the head and neck of the tibia; its tendon passes through the transverse ligament and the bony bridge just above the intertarsal joint; it then runs down on the anterior surface of the metatarsal bone, and sends a tendon to the dorsal part of the bases of the phalanges of the three front toes. The mode of splitting up of the common tendon into the special tendons and of their insertion varies much.

*M. perforatus digiti* II.—This muscle appears after the removal of the most superficial of the flexor muscles on the outer side of the leg. It comes with fleshy fibres from the ligam. fem. tibiale externum and from the hinder part of the neck of the tibia. Its long and slender tendon, after crossing the legs, passes right through the susceptaculum in the middle of the hinder aspect of the intertarsal joint, where it lies deeper than all the other tendons. It is inserted into the ventral side of the phalanges II. et III. digiti II.

*M. perforatus digiti* III. consists of two very fleshy heads. The *outer* one is completely fused with that of the m. perforatus dig. II.; it arises partly from the external condyle of the femur and from the tendinous loop; one part of this head forms the continuation of the tendon of the ambiens muscle. The *inner* head arises with a distinct tendon from the hinder aspect of the middle part of the intercondyloid region.

The combined tendon of the whole muscle, when passing over the intertarsal joint, is quite flat, and lies between the susceptaculum and the broad tendon of the gastrocnemius muscle. Thus in this region it is the most superficial of all the flexor tendons. At the middle of the metatarsal bone the tendon gives off a slip to that of the m. perforans et perforatus dig. III.

*M. flex. perforatus dig.* IV.—Its thick belly arises from the hinder aspect of the external condyle of the femur and from the intercondyloid region. Its tendon, simply covered by the tendo Achillis, passes as the most superficial one over the joint and is inserted into the basis phal. II. dig. IV.

The *m. flex. perforans et perforatus dig.* III. arises with a long slender head together with the m. perforatus dig. III. and with the m. perforatus dig. II.; its tendon sends a slip to that of the m. perforatus, which it also perforates, and is inserted into the bas. phal. II. et III. dig. III.; on the other hand, this tendon is pierced by that of the m. flexor profundus.

*M. flex. perforans et perforatus dig.* II.—The strong and fleshy belly of this muscle arises with a short tendon from the hinder plane of the intercondyloid region; it passes through a special canal in the susceptaculum, and is one of the deepest muscles. It is inserted into the cap. phal. I. dig. II.

The *m. flex. profundus s. communis digitorum* consists of two principal heads. The *outer* one arises with fleshy fibres from the fibula and is partly fused with the m. tibialis; its strong tendon passes the intertarsal joint superficially to the susceptaculum, and is only covered by the tendo Achillis; it passes the pulley on its outer or lateral, not on its ventral or posterior margin. The *inner* or chief head takes its origin from the hinder plane of the greater part of the tibia; its tendon runs as the deepest of all through the pulley, and then unites with that of the outer head; the tendon then divides into three, each of which is inserted into the basis of the last or distal phalanx of the II., III., or IV. digit.

Although *Pterocles* possesses a rudimentary hallux, which consists of two very small bones not articulated with the metatarsus, there was no trace of a *m. flexor hallucis longus* to be found. But there was a *m. flexor hallucis brevis*, which arose from the hinder aspect of rather more than the upper two thirds of the tarso-metatarsal bone, and was inserted into the cap. phal. I. dig. I.

An *abductor brevis. dig.* IV. and an *abductor brevis dig.* II. were likewise present—the former pulling the fourth toe inwards, *i. e.* towards, the latter drawing the second the away from the middle one. Both consequently move these two toes tibiad, and are morphologically abductors.

For the *m. flexor brevis dig.* III. see note, § 4.

*Note.*—Mr. Forbes has kindly drawn my attention to Mr. A. Haswell's paper "Notes on the Anatomy of Birds. III. The myological characters of the Columbidæ," in Proc. Linn. Soc. New South Wales, 1880, p. 306; and has expressed grave doubts about the correctness of some of the statements made in it. Mr. Haswell, at the end of his paper, mentions five points "which seem to be especially characteristic of the family." But I find that of the five points, one is totally incorrect, and three others, viz. nos. 3, 4, 5, are not characteristic of the Columbidæ. These points are:—

1. The absence of a posterior belly of the m. latissimus dorsi. Mr. Forbes and I, on examining the following birds, which were at hand—*Carpophaga, Chalcophaps,* and *Columba*—found this muscle consisting of two bellies, the posterior one being just as well developed in these Pigeons as in *Astur,* arising from the anterior margin of the ilium and from the last dorsal vertebræ, and inserted by means of a tendon below that of the anterior belly into the humerus. Throughout their whole length the two bellies were connected by a fascia.

3. The absence of the m. glut. externus and the presence of the adductores brevis et longus, the semitendinosus and semimembranosus. Now the m. gluteus externus (=*glut. anterior*) is generally very small, but plainly visible in many birds, such as Pigeons, Passerine birds, &c., and not absent as stated by Mr. Haswell.

The four other muscles are well developed in most birds, as Prof. Garrod has stated over and over again, and as the dissection of any fowl will show.

4. "The special relation of the tendon of the ambiens (when present) to the fibular head of the flexor perforatus secundus tertii digiti." The distal end of the ambiens muscle, when typically developed, always forms the continuation of one of the heads of the m. flexor perforatus dig. II. et III.

5. "The presence of lumbricales in the foot." The muscle which Mr. Haswell takes to be the representative of the lumbricales muscles of mammals has not "hitherto escaped the notice of anatomists," and it is not "peculiar to the Pigeons," since it is also present in many other birds, *e. g.* the Ratitæ, and has been described by Meckel, although he gave no name to it, in his 'System der vergleich. Anat.' iii. p. 388, and in his 'Archiv für Anat. u. Physiol.' pp. 278 & 279.

With regard to the muscles of the leg, I am unable to point out any typical differences between Sand-Grouse, Fowls, and Pigeons. The absence of the m. flexor hallucis longus in *Pterocles* is of no importance, as this muscle is generally absent in birds which have no hallux or only a small one, and, moreover, as the absence of this toe itself affords no family character. Of course there are many points, *e. g.* the mode of origin and the arrangement of the tendons of the muscles, and even the absence of the m. plantaris and of the m. peroneus profundus, which are noteworthy in *Pterocles*; but all these things are variable, and give us no characters which hold good throughout the Gallinaceous or the Columbine group.

It is the same with the m. ambiens: this muscle is present and well developed in *Pterocles* and most probably in all the Rasores; in the Pigeons its presence is variable.

Of all the other muscles connected with the leg, there is none that shows any practical difference between Sand-Grouse, Pigeons, and Fowls, and even (if we include them in our comparison) the Plovers.

On the whole, however, the myology of *Pterocles* indicates that it is more nearly allied to the Pigeons than to any other group of birds.

## Viscera.

"The trachea is cartilaginous; and it has at its bifurcation what the Grouse is bereft of, viz. a pair of laryngeal muscles, as in the Pigeons, *Talegalla*, and Plover" (*Parker*).

The *crop* (*ingluvies*) of *Pterocles* is a simple dilatation of the anterior and lateral walls of the œsophagus, without any constriction in the middle line, although it is broader than long. Its walls are very thin on its anterior parts, and show longitudinal folds and glands; the dorsal part, the prolongation of the dorsal half of the œsophagus, is thicker and slightly muscular, the external sheath consisting of transverse, the inner one of longitudinal smooth muscular fibres.

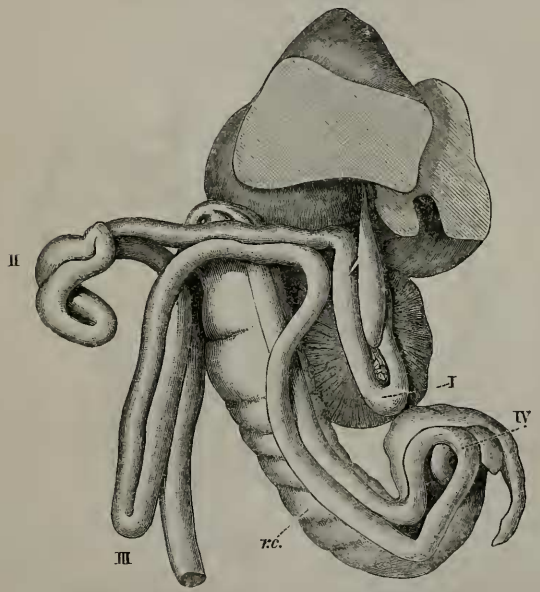
In the Pigeons the crop is different. It consists of two lateral and symmetrical dilatations of the lateral walls, whilst the middle part is simply the continuation of the œsophagus, slightly widened

out at the upper and lower end of the crop. The glands are nearly equally distributed over the inner lining of its walls, and are arranged in very irregular longitudinal folds.

The *proventriculus* of *Pterocles* is a long oval, and comparatively small; its walls are thick and full of glands, which are "ovoidal and simple as in the Pigeon and Plover, not botryoidal as in the Grouse and Fowls."

The *ventriculus* or *gizzard* is of a subquadrangular shape, much flattened and very muscular, showing on the right and on the left side a speculum tendinosum; the posterior wall is deeply bent in

Fig. 3.




Right lateral view of intestines of *Pterocles arenarius*.
*rc*, right cæcum; I, II, III, IV, intestinal loops.

towards the middle line. Its inner lining consists of a hardened and much thickened excreted mass, without however forming any distinct triturating planes.

The *duodenum*, *ileum*, and *rectum* form four distinct "closed" loops, which are arranged as follows:—The first, or duodenal loop is very short and straight, as it only extends over the posterior margin of the gizzard; its diameter is slightly larger than that of the ileum; the length of the duodenal loop in *Pterocles* is about 4·5

centim. The second loop is nearly double the length of the first, and has its apex doubled up into an irregular knot, as is characteristic of the Gallinacei proper. The third loop is of about the same length but straighter. The fourth loop is almost three times as long as the duodenal one; it is stowed away in the most ventral and lowest part of the abdominal cavity, between the gizzard and the vent; throughout its whole length it is accompanied by the two cæca, which are closely attached to this loop, as they are supplied by the same branch of the mesenteric artery. The rectal part of the intestinal tract is slightly wider than the ileum and the duodenum.

The *cæca* (see fig. 4) are extremely well developed in *Pterocles*, being 16 centim. long, and are inserted at a distance of 15 centim. from the anus. They are very wide and have very thin walls; their

Fig. 4.


*a*, Cæca of *Pterocles arenarius*; *b*, Cæca of *Syrrhaptes paradoxus* (after Brandt).

inner lining forms about 6 longitudinal slightly elevated folds. (Prof. Parker says that the cæca of the Sand-Grouse have 12 longitudinal folds, not 7 as have the Ptarmigans.)

The cæca of *Syrrhaptes*, according to Brandt, are very wide and long too, but differ from these organs of *Pterocles* in the shape of their terminal parts, as shown in fig. 4.

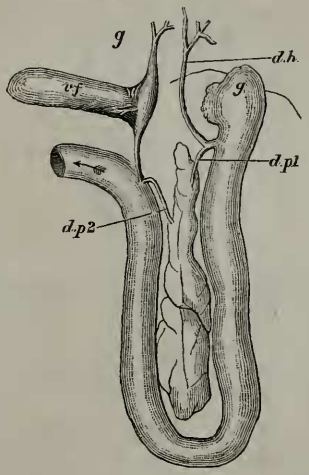
The *liver* of *Pterocles* I found to consist of two principal lobes—the right lobe being about three times larger than the left one, which exhibits on its inner side a small Spigelian lobe. The sharp

lower edges of both lobes have several slight emarginations; and there is a strong commissure between the lobes.

The *gall-bladder* in my specimen of *Pterocles* is large, forming a very distinct cylindrical lateral pouch; its cystic duct opened into the ascending end of the duodenal loop, whilst the hepatic duct was inserted opposite to the cystic duct, just below the pylorus.

This arrangement of the ducts, however, seems to be subject to much variation; for Prof. Brandt found that the cystic duct in *Syrrhaptes* either opened into the terminal part of the duodenal

Fig. 5.




Duodenum of *Pterocles arenarius*, with the bile- and pancreatic ducts.

loop, together with the hepatic duct, or in other cases near the pylorus, when the hepatic duct was inserted into the duodenum opposite the pylorus. (See figs. 5, 6, 7.)

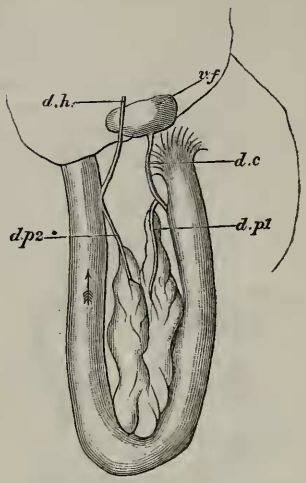
The *pancreas* in *Pterocles* and in *Syrrhaptes* opened by two ducts, one into that bile-duct which was inserted near the pylorus, the second just in front of the other bile-duct.

The arrangement therefore was as follows:—

*Pterocles arenarius*: d. hepatic + 1st d. pancreat. inserted near the pylorus.
2nd d. pancreat. + d. cystic (see fig. 5) inserted opposite the pylorus.

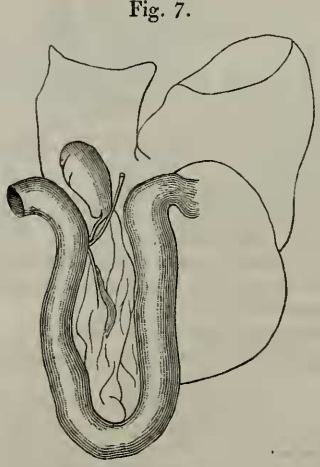
I. *Syrrhaptes paradoxus*: 1st d. pancreat. + d. cyst. inserted near the pylorus (fig. 6).
2nd d. pancreat. + d. hepat. inserted opposite the pylorus.

Fig. 6.




Duodenum of *Syrrhaptes paradoxus*, with bile- and pancreatic ducts (after Brandt).

Fig. 7.



Duodenum of *Syrrhaptes paradoxus*, with bile- and pancreatic ducts (after Brandt).

II. *Syrrhaptes paradoxus*: 1st d. pancreat. inserted near the pylorus (fig. 7).
2nd d. pancreat., +d. hepat. +d. cystic. inserted opposite the pylorus.

| | Total length of gut. | Relative length.[1] | Length of cæcum. | Distance of cæca from anus. |
|---|---|---|---|---|
| | centim. | | centim. | centim. |
| Pterocles arenarius ..... | 83 | 7–8 | 16 | 15 |
| —— ——(after Brandt) | 80 | | 15·5 & 18·5 | 12 |
| Syrrhaptes (after Brandt) | 87 | ... | ... | 13 |
| Perdicula cambayensis ... | 38–42 | 6–7 | 5 | 3–4 |
| Perdix cinerea ..... | 75 | 8 | 17 | 6 |
| Phasianus pictus ..... | 106 | 7·5 | 10–15 | 8–12 |
| —— swinhoei ..... | 106 | 7 | 13 | 7 |
| Euplocamus prælata..... | 122–152 | 7–7·5 | 22 & 23 | 8–12 |
| Crax alberti ..... | 222 | 9 | 10 & 14 | 15 |
| Columba livia ..... | 96–125 | 12–13 | 0·5–0·8 | 4–5 |
| Calœnas nicobarica ..... | 125 | 10–11 | 0 | |
| Peristera geoffroii ..... | 34 | 4 | 0·3 | 4 |
| Erythrœnas pulcherrima | 41 | 5·5 | 0 | |

The liver of the Rasores, as well as that of the Columbæ, is quite different. The left lobe is divided again into two by a deep fissure, so that the whole organ might be called trilobed. The right lobe is generally the larger; a Spigelian lobe is present in most of these birds. The outline of the lower margin varies much in the different Fowls and Pigeons.

The existence of a *gall-bladder* in the Pterocletes might be looked upon as a strong indication of difference between them and the Pigeons, as in the Gallinaceous birds this organ as a rule is well developed. However, it must not be forgotten that in several typical Rasores, as in *Euplocamus*, *Numida*, and *Penelope*, there is sometimes scarcely any pouch-like dilatation of the bile-ducts. In the Rasores the cæca are, without any exception, very well developed, and have mostly an extremely large and wide lumen. The length of both the cæca compared with the length of the intestinal tract (from pylorus to anus) is in the proportion of 1 : 7 (*Crax*), or even 1 : 2·2 (*Perdix*). In the Pigeons, on the other hand, the cæca are always in a rudimentary condition, their sum total being in the proportion of 1 : 75 in our domestic Pigeon, and 1 : ∞ in *Goura*, *Calœnas*, *Chalcophaps* &c., as they are either completely wanting in most of the Columbæ, or are only represented by very small, often barely visible, vermiform-like appendages.

It has sometimes been stated that Pigeons have to rank with such birds as do possess cæca, because such organs, although very small,

[1] See my paper in the 'Jenaische Zeitschrift für Naturwissenschaft,' 1879, p. 369.

exist in our common Pigeon, and thus they are in contrast with those birds in which cæca are altogether wanting, like Woodpeckers, Parrots, and others. Garrod likewise included the Passerine birds amongst the Menotyphla (to use a Hæckelian term for animals possessing cæca). Now I think this is not correct; and we must consider this matter a little further. Garrod himself came to the conclusion that the ancestral bird-stock did possess cæca; as this is undoubtedly true, it follows that all those birds which are now found without cæca must have lost them, either phylogenetically or even during their ontogenetic development. In fact we see, in embryos of such birds as have when adult only very small quite rudimentary cæca, that these organs are, in the embryo, just as well developed as in birds with long cæca; but these cæca, in a Pigeon for instance, do not grow any further. They are in early life stopped in their development, and thus remain in a rudimentary state. Again, in all those birds which are completely devoid of cæca the tendency to suppress these organs is simply carried out to the extreme. We cannot, therefore, group the birds into birds with cæca and birds without cæca; and this is especially wrong, as there exist many birds which, although apparently allied to each other, differ greatly in the presence or absence of cæca.

If we want to take the cæca into consideration at all, we must take another point of view: that is, are the cæca of any use to the birds in question or are they not? Now, apparently, in all birds which have well-developed cæca they are useful, although we must confess that we do not know in what way. Again, in birds with very small cæca, where these organs are simply vermiform-like processes, and which never contain any chyle in their extremely small lumen, they cannot have any physiological function, else they would not have been suppressed.

No doubt in some cases, in which they are not quite aborted, as for instance in the Crows and in our common Pigeon, the glands in their walls may still produce some secretion, which then may be made the best of. But this is one of the cases in which rudimentary organs are not completely stopped in their functions although they are useless, simply because the animal hitherto has not been able to get rid of them entirely: thus, for instance, the appendix vermiformis of man, or another example still more striking, our thymus gland, which, although a gland, is now without a duct, and thus rather a paradox.

But to return to our question. It is clear that birds with rudimentary cæca have to be grouped together with lipotyphlous birds, *i. e.* birds which have lost these organs.

The great development of the cæca therefore constitutes a considerable difference between the Pteroclidæ and the Columbidæ, as the former and the Gallinacei are decidedly menotyphlous and the Columbæ lipotyphlous.

In the Gallinacei the whole digestive tract always forms four very distinct loops: the duodenal one is the first; the next two loops are formed by the ileum; in birds which, like *Perdix*, have a compara-

tively short gut, these two loops are very short, and are stowed away on the right side of the abdominal cavity; when the ileum is relatively long, the number of the loops is not increased nor do the two loops grow in a straight direction, but the apex of each turns backwards so as to give the loops a horseshoe shape. The fourth loop is formed by the last third of the ileum, and is accompanied by the cæca; the whole loop is never a "closed" one, its terminal branch is nearly straight, the other one much shorter and, if the gut be long, irregularly curled.

We meet with a totally different arrangement in the Columbæ. There are invariably only three loops formed by the intestinal tract. The first, the duodenum, is very wide, and sacculated at the apex. The second is very long, and, in all those species where the total length of the intestine is not (as for instance in the fruit-eating *Carpophaga latrans*) extremely short, is entirely coiled up into a left-handed spiral. As a rule there are in this spiral 3 direct and 2 retrograde turns; the number of these, however, wholly depends on the relative length of the ileum: thus in the common Pigeon, with the relative length of the gut about 12, the apex of the ileum-loop has turned round $3\frac{1}{2}$ times; whilst in others, like *Chalcophaps*, the number is less; and, lastly, in Pigeons with very short guts, as in *Carpophaga*, a spiral is not developed at all (because, as far as we know at present, the intestinal spiral in certain birds is only one of the means of stowing away the longitudinally growing gut). But it must not be forgotten that in *Columba* as well as in *Carpophaga*, whether the ileum be long or short, we never have more or less than three folds. The last, or third loop is a very long one too, entirely closed or double throughout its whole length.

## Mode of Life and Propagation.

The Sand-Grouse differ greatly from the Pigeons in their mode of *drinking*. It is well known that the latter, during the act of drinking, dip their bill into the water as far as the cleft of the mouth, and then suck the water in without raising their head till they have finished drinking. *Pterocles* and *Syrrhaptes*, on the other hand, drink as Fowls and other birds do, by taking up water mouthful by mouthful and letting it run down the throat. This peculiarity is probably the result of a special mechanism of the muscles of the throat and glottis, but is as yet unexplained.

Their flight consists of rapid uniform movements of the wings, and generally resembles that of the Pigeons more than that of the Plovers; but they do not glide or soar as the Pigeons do.

From their voice we cannot gather much information as to their affinities; but certainly they do not coo.

During the greater part of the year they are gregarious. They are monogamous like Pigeons and Plovers, differing in this respect greatly from the Rasores, which are typically polygamous. Their nest is extremely simple and situated on the ground. The number of eggs laid by *Pterocles* is three; while according to Radde *Syr-*

*rhaptes* lays four, which in general appearance and so-called structure resemble those of certain Partridges.

The Plovers lay the same number. The Pigeons, on the other hand, invariably lay only two; and this is so characteristic of the whole group that Bonaparte named them Bipositores. Again, all the true Gallinaceous birds produce a great and indefinite number of eggs. Therefore in this respect the Sand-Grouse are more nearly allied to the Plovers than either to Grouse or Pigeons.

According to an observation made in the Zoological Gardens of London in August 1865, the period of hatching seems to be a little more than three weeks: two eggs were laid at the beginning of August; and the young birds came out on the 29th of the same month.

But one of the most valuable points, as regards the systematic position of the Pterocletes, is the fact that the young when hatched are thickly covered with hairy down, and that as soon as their plumage has dried they are able to leave the nest and seek their food. This removes them far from the Pigeons, which are the most decided pædotrophic or gymnogenous of all the birds we know.

Now to sum up. We have seen that there are many points in which the Pteroclidæ have striking resemblances to the Columbidæ; but there are also many points in which they approach the Rasores; and it is difficult, if not impossible, to made out which characters are the more important.

Prof. Parker was the first to point out clearly that there is a relationship between Sand-Grouse and Plovers; and Prof. Garrod, in his classification of birds, groups the Columbæ, including Pteroclidæ, and the Limicolæ, including Charadriidæ, together under his order Charadriiformes. But the Columbidæ undoubtedly are related to the Rasores through such forms as the Cracidæ (*Peristeropodes*, Huxley) and the Tetraonidæ; and, in addition, they are linked together by *Pterocles* and *Syrrhaptes*. These circumstances show that there exists a close relationship between Rasores, Columbæ, Pterocletes, and Limicolæ. Phylogenetic tables as a rule are faulty from being highly hypothetical, and from the imagination being frequently drawn upon in their compilation. However, they can be useful, even if they only show where our knowledge is yet insufficient, or why systems hitherto made do not agree with more recent ideas. Therefore I venture to draw the outlines of a branch of the avian stock, not led by preconceived ideas, but solely guided by the consideration of facts we know, or at least we have a certain right to believe we know.

1. Rasores, Columbæ, and Limicolæ are nearer related to one another than to the rest of the birds.

2. If the Columbæ approach nearer to the Charadrii than to the Rasores, we can express this idea by a stock which gives off two main branches:—one for the Rasores; and another one which again soon divides into two—one Columbine, and one for the Plovers (see fig. 8).

3. As the Pigeons have closer affinities to the Fowls than the latter have to the Plovers, the Pigeons must be represented by the middle branch, that to the extreme left remaining for the Plovers.

4. The most specialized of the Rasores (that is to say, the typical Alectoromorphæ) we have to put at the end of the right branch. The Tetraonidæ and the Cracidæ are those which, of all the Rasores, show the greatest resemblance to other families; they must therefore form the earliest or lowest twigs of the Rasorial branch; consequently we have to put their special roots nearest to the biggest and at the same time more indifferent stock.

But now as to *Pterocles*.

1. No doubt the Sand-Grouse are more nearly allied to the Rasores than the Pigeons are. Consequently we must seek for their root between the Rasorial and the Columbine branch.

2. Again, the Sand-Grouse are more nearly allied to the Pigeons than to the Plovers; thus their branch must be put nearer to the Columbine branch than to that of the Plovers.

Fig. 8.

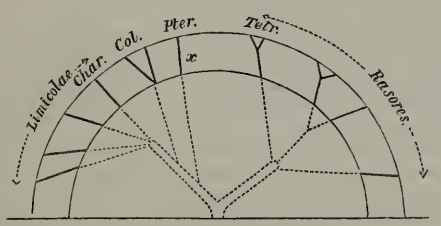



Diagram showing the supposed relationship of the Pteroclidæ.

This conclusion and the former can be reconciled only if we put the Sand-Grouse branch at $x$; and as this places them pretty nearly in the centre of our hypothetical table, it proves that our final conclusion cannot be far from right.

The fact is that birds just a little less specialized than *Pterocles* —in other words the direct ancestors of *Pterocles*—would contain all that is necessary to develop them into either Fowls, Pigeons, or Plovers.

Considering these circumstances, we see once more that, as Macgillivray and Professors Sundevall and Garrod have maintained, the Pigeons are not so closely related to the Fowls as is generally supposed.

It would be extremely difficult to arrange the birds represented in our table into families and groups as is required in a practical system. If we want to divide them into only three groups—Plovers, Pigeons, and Fowls—of course *Pterocles* has to go with the Pigeons; but this would not express its close relationship to the Tetraonidæ. Again, we cannot include the Pigeons and Fowls under one large group, and the Plovers under a second, because the Pigeons must be placed along with the latter. And Pigeons and Plovers cannot form one

large group and the Fowls the other, because then this Plover-Pigeon group would include a form, viz. *Pterocles*, which we know to be more closely allied to the Rasores than to *Charadrius*. It must also be remembered that Snipes and Gulls are closely related to the Plovers; and of course *Pterocles* cannot be placed in such a position as would indicate that it is more closely related to the Gulls than to the Grouse. Thus it will be best to make a group or family Pterocletes, as Mr. Sclater has done, coordinate with those of Pigeons, Plovers, Gull, Fowls, and the like.

On the other hand, if we are to answer the straightforward question Is *Pterocles* more nearly allied through its ancestors to the Pigeons or to the Fowls? we are compelled to say that they are nearest to the Pigeons. Of course they have many features in common with the Fowls; but in no case we can include them under the latter, for the following reasons:—

*Pterocles* shows some, although only a few, anatomical points which we only find amongst the Columbidæ, whilst all the other numerous points in which it resembles the Fowls are such as must have been common to the old ancestral Stork, as we find them again in some of the Limicolæ. But some of its Columbine features it is impossible to trace so far back, as they indicate a very high degree of specialization. *Pterocles* must have branched off from those birds which we may term "incipient Pigeons," and then, for reasons we can only suggest (perhaps similar conditions of life, and the like), have preserved and developed many of those old characters which the Fowls have also inherited from the same source, and have them developed in a similar way, as living under the same conditions.

The main part of the ancestral or incipient Pigeons at the same time started in another direction, losing, as they proceeded, many of the old characters[1], and acquiring numerous new ones, till they became that highly specialized group which is now called Columbæ.

[1] Among the most important characters common to the ancestral stock which the Pigeons have lost, or are in process of losing, are the following:—

1. The Pigeons have nearly completely lost the cæcal appendages of the rectum.

2. There seems to be a tendency to lose the ambiens muscle, as in many of the Pigeons it is completely absent, and in others this muscle is unstable in its presence.

3. They have lost the aftershaft to the feathers.

4. They have almost completely lost their nestling plumage, and the old character of being autophagous birds, as their young are now hatched nearly nude, blind, utterly helpless, and depending entirely on their parents, and have to spend a considerable part of their childhood in a very imperfect state.